

CRATERODISCUS McMICHAEL, 1959,
A CAMAENID LAND SNAIL FROM QUEENSLAND

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Plate 37

SUMMARY

Dissection of *Craterodiscus pricei* McMichael, 1959 shows that it cannot be classified in the Helicarionidae as originally suggested. It appears to be the most primitive species of the helicacean land snails yet dissected and is referred tentatively to the Camaenidae, s.l. Scanning electron microscope studies of the radula revealed that it has one of the most remarkable cusp structures found in a pulmonate snail.

INTRODUCTION

McMichael (1959) described a new species and genus of land snail from Hypipamee Crater, Atherton Tableland, North Queensland, Australia as *Craterodiscus pricei*. On the basic shell structure he compared it with the Queensland endemic *Theskelomensor* and temporarily placed it in the Helicarionidae. Through the courtesy of Mr. Laurie Price of Kaitaia, New Zealand, I obtained preserved topotypes of this species that were collected in August 1964 (Field Museum of Natural History number 135141).

As part of a long range review of endodontid genera from the Pacific Islands and the Austro-Zelandic region, *Craterodiscus* was dissected in order to check on the possibility that it was an aberrant endodontoid derivative. Much to my surprise this turned out to be a member of the Helicacea with several quite primitive anatomical features.

This report attempts both to record its unusual structure and to place it within generally recognized family limits. There is no agreement concerning family level units for Australian land snails. A very conservative course is followed here by placing it in the Camaenidae, s.l. When anatomical knowledge of the Australian Helicacea is more advanced, an alteration of family units may be required.

SHELL STRUCTURE

Specimens ranged from 4.9 - 5.2 mm. in diameter with 6 to 6½ whorls. The whorls show only modest increase in width from the first whorl (0.33 mm. wide) to the body whorl (0.58 mm. wide). Since this is coupled with a quite widely open umbilicus (contained 2.2 - 2.5 times in the diameter), there is very little cross-sectional area difference between the early post-nuclear whorls and body whorl (see figures in McMichael, 1959). Compared with more typical Australian helicoid shells such as *Hadra*, *Austrochloritis*, *Sinumelon* or even *Pedinogyra*, where the whorls rapidly enlarge in cross-sectional area, it seems very atypical in form. When combined with the absence of any lip reflection or callus formation to indicate terminal growth or slowing of growth upon becoming reproduc-

tively mature, reference to the Helicarionidae was a logical suggestion. Many taxa in this family have a comparatively high number of whorls that are tightly coiled, lack any positive indication of adult shell growth changes, and also lack any marked surface sculpture on the shell.

Both the relatively high whorl count and the small cross-sectional area increment in *Craterodiscus* have affected anatomical structures. Hence emphasis on the somewhat unusual shell form is necessary preamble to a discussion of the anatomy.

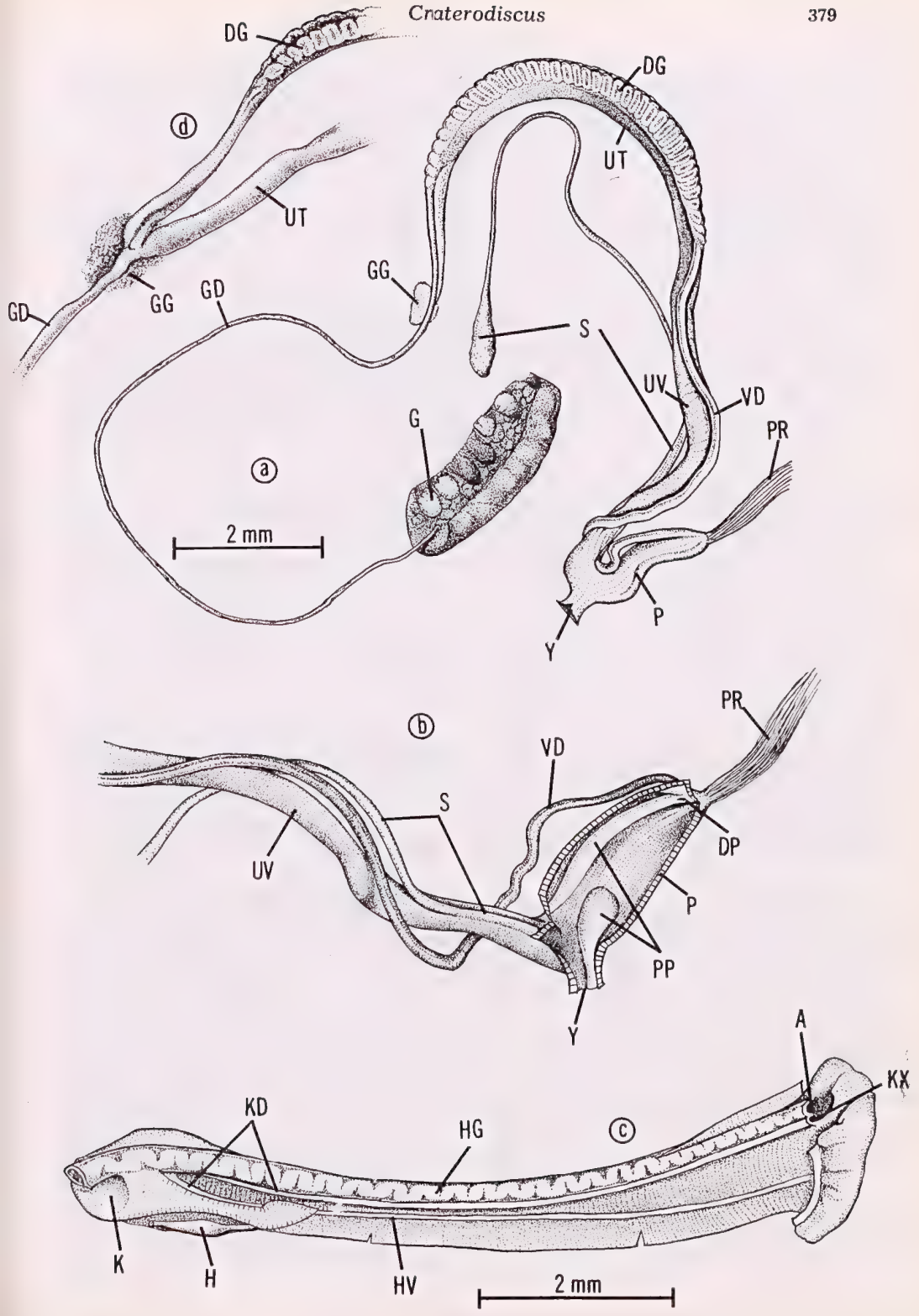
DESCRIPTION OF GROSS ANATOMY

Externally the body is colorless, except for grey speckling on the ommatophores and relatively large black eyespots. Foot and tail truncated anteriorly, bluntly rounded at posterior end with noticeable transverse corrugations in most examples. Slime network irregular on head and sides of foot, becoming relatively elongated and rectangular just above foot margin. The character of the foot is holopod, not aulacopod. Gonopore location is below right ommatophore and behind right rhinophore.

Pallial region (Fig. 1, c) extending apically about one whorl in expanded specimens. Kidney (K) extending as dished posterior portion well over intestinal loop, quite narrow, reaching hindgut for posterior third of length, not bilobed, anterior end partly lying under primary ureter and pulmonary vein (HV). Latter extending anteriorly to edge of mantle collar, well removed from hindgut and markedly diverging from same in anterior half. Heart (H) very narrow, almost two-thirds length of kidney. Ureter (KD) angled backwards along upper edge of kidney to hindgut, then reflexing forward to external ureteric pore (KX) directly alongside anal pore (A) at pneumostome.

Genitalia (Fig. 1, a, b, d) characterized by elongation and narrowing of parts together with little fusion of the male and female tracts. Otestis (G) of weakly divided lobes imbedded in digestive gland at upper palatal margin from one-eighth to one-quarter whorl above stomach, connecting to single tubule that leads into a very long hermaphroditic duct (GD). Latter following the prolonged stomach at parietal-palatal margin for almost one and one-half whorls, no major change in size or texture. Albumen gland (GG) variable in size, nestled between loops of intestine, with very fine acinar structure. No differentiation (Fig. 1, d) of a talon or distinct carrefour structure. Details of union between hermaphroditic duct (GD), albumen gland (GG) and separation into prostatic gonoduct (DG) and uterine gonoduct (UT) requiring histological study for elucidation. Split into totally separated male and female tracts (Fig. 1, d) occurs above pallial cavity apex. Prostatic and uterine gonoducts appressed together along pallial passage, but not at all connected. Free oviduct (UV) and uterine oviduct (UT) not externally differentiated, arbitrarily distinguishable in labelling at point where prostatic acini end and simple vas deferens (VD) continues down to peni-oviducal angle.

Text Fig. 1. Anatomy of *Craterodiscus pricei* McMichael (FMNH 135141). (a) genitalia showing origins and insertions of organs, (b) details of terminal genitalia and interior of penis, (c) pallial region, and (d) details of postpallial and early pallial genitalia showing complete separation of pallial gonoducts. Figures (b) and (d) enlarged over the scales shown for (a). Drawings (a-c) by Miss Claire Vanderslice, (d) by Miss Nelva Bonucchi.



Penial retractor (PR) inserting on head of penis, arising on lower part of pallial diaphragm. Vas deferens (Fig. 1, b) entering penis (P) near apex through a simple pore (DP) that lies in middle of a longitudinal pilaster (PP) that continues to atrium (Y). On lower third of penis interior, a second, higher, drop-shaped pilaster originates and continues down to base of atrium. Spermathecal head (S) slightly and elongately expanded, lying next to albumen gland, very slender shaft gradually fusing with free oviduct (Fig. 37, b) just above atrium so that no vaginal area differentiated.

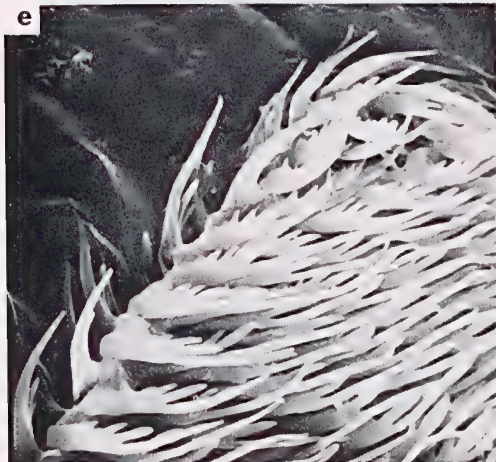
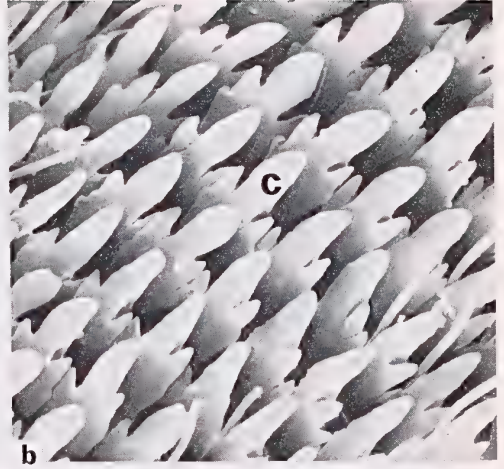
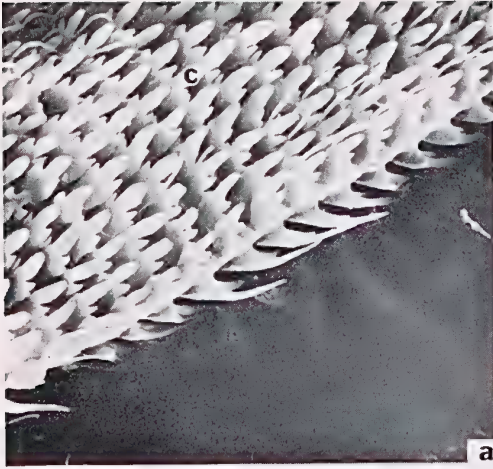
Radula (Pl. 37) very distinctive with development of extraordinary endoconal cusp extensions on outer lateral and marginal teeth. Central tooth (Pl. 37 a, b, identified by "C") tricuspid, mesocone extending to level of ectoconal base on tooth in posterior row, ectocones variable, but usually coequal in size. First laterals with endocone distinctly narrower and shorter than ectocone, mesocone often noticeably slenderer than mesocone of central tooth. Second lateral with ectocone split, endocone narrowed and slightly elongated. Third lateral with endocone extended into a slender lance-like prolongation (Pl. 37, c). Subsequent laterals with greater elongation of the endocone (Pl. 37, d). Transition to marginals involving progressive reduction of the mesocone, elongation of endoconal prolongation and finally increased splitting of the ectocone. Marginal teeth (Pl. 37, e, f) presenting a forest of endoconal prolongations, subsidiary cusps prolonged and elevated. In Pl. 37, figs. a-d are from the left anterior side of a radula, figs. e-f from the right posterior side of the same radular mount. Hence the difference in wear and cusp loss between the teeth in the two series of photographs.

Based on four specimens from Field Museum of Natural History number 135141.

DISCUSSION OF ANATOMICAL FEATURES

As is common in many taxa having increased whorl counts, the apex of the soft parts was located $2\frac{1}{2}$ whorls below the shell apex. The apical whorl space was filled with solidified mucous. As growth proceeded the apex of the digestive gland would have to be gradually withdrawn from the shell apex leaving empty space behind. Whether this is used by the snail for water storage or is simply an unutilized area is unknown. An unusually heavy amount of mucous was found alongside the soft parts at every level of the visceral hump. Probably this relates to the withdrawal of soft parts from the early whorls. Although whorl expansion is minimal, as pointed out above, there still is more cross-sectional area lower in the spire than at the apex. Withdrawal of the soft parts from a "fitted space" into a wider area leaves room around the body that the mucous partly fills.

Several features of the anatomy probably relate to the narrow whorl cross-section and can be assigned no phyletic significance. The narrowing and elongation of the kidney, the very long hermaphroditic duct, and peculiar path of the pulmonary vein on the lower part of the pallial roof, are all adaptations to narrow whorls. In order to allow full retraction of



the head and foot into a shell with narrow whorls, the kidney often is narrowed, extended apicad over the intestinal loop, and squeezed up into the parietal-palatal margin. This maximizes the area in the pallial cavity and allows more complete body contraction. The kidney form and position in *Craterodiscus* is typical of this alteration in pattern. Thus the position of the pulmonary vein relative to the hindgut in the anterior portion of the pallial roof probably is a relict from a "normal" shelled ancestor, while its close approach posteriorly, the shape of the kidney, and the vein-ureter-kidney overlap represent a space accommodation of recent origin. Narrowing of the whorls requires elongation of the stomach to maintain equivalent stomach volume to body volume ratio. With this, the hermaphroditic duct, a space saving tube connecting the ovotestis with the fertilization area, simply elongates equally.

Other anatomical features are not space correlated and hence can be given greater phyletic weight. The absence of fusion between the prostatic and uterine gonoducts throughout the pallial region is a primitive character in land snails. In such aulacopod taxa as the Helicarionidae, the Microcystinae have split pallial gonoducts, while the more advanced Helicarioninae, for example, have fusion of pallial gonoducts into a "sperm-oviduct." Primitive Orthurethra, such as the Tornatellinidae, have split pallial gonoducts, while in the more advanced Pupillidae there is partial fusion of the pallial ducts. The change from split to fused has occurred several times independently. Lack of any differentiation into an epiphallic section by the vas deferens also generally is a primitive character, although of much less phyletic significance. In cases of whorl reduction, a preliminary stage in evolution of slugs from shell-bearing taxa, then secondary reduction of the epiphallus or morphological infolding of this into the penis is of common occurrence. In cases of whorl increment, I have seen no evidence for changes in the epiphallic structures occurring. Hence the lack of an epiphallic section in *Craterodiscus* may well be a primitive feature. This also suggests that sperm transfer is not by use of a spermatophore or sperm packet. Finally, there is the holopod nature of the foot. While in a few genera, such as the Bermudan *Poecilozonites*, aulacopod snails have developed a holopod foot situation, details of genital and radular structures leave no question as to the actual affinities.

Radular structures of the central and early lateral teeth are not unusual, but I know of nothing in the stylommatophoran pulmonates comparable to the endoconal prolongations found in *Craterodiscus*. Temporarily ignoring these, the basic characteristics of the radular teeth are the rather squarish to rectangular basal plates of the teeth, and the multicuspoid nature of the marginals. In the marginals, the basal plates are shortened, but still square in form (Pl. 37, e), and the cusps inclined centrally.

AFFINITIES OF CRATERODISCUS

Consideration of the currently accepted diagnostic features for stylommatophoran classification immediately excludes *Craterodiscus* from several major groupings. The pallial configuration with secondary ureter places this within the Sigmurethra. Both the holopod foot and the confirmatory structures of the radular marginal teeth exclude classifying it with the aulacopod superfamilies Limacacea and Arionacea. Radular basal plate structures in the Limacacea are elongately rectangular with generally bicu-

Craterodiscus

spid (Zonitidae) to multi-cuspid (Helicarionidae) marginal configurations. In the Arionacea, the marginal teeth basal plates, with very few exceptions, are much wider than they are long, although retaining a rectangular shape. The small, square marginal basal plates with multi-cuspid denticles of *Craterodiscus* are quite different.

Thus *Craterodiscus* should be grouped with the holopod sub-group of the Sigmurethra. The various carnivorous taxa plus such herbivorous groups as the Bulimulacea, Achatinacea, and the sigmurethrous acavacean genera show such major differences in pallial structures, genitalia and radular characters that no discussion of detailed differences seems necessary. When added to the gross discrepancy in size (acavaceans) and totally different shell form (Achatinacea and Bulimulacea), these possibilities can be dismissed.

This leaves three superfamily groupings for consideration, the Polygyracea (including the Corillidae), the Camaenacea, and the Helicacea. In the first, the radular structure is basically bicuspid with the marginal basal plates tending to become rectangular with their width greater than their length. In the Helicacea, the radula is basically tricuspid with squarish basal plates. In the Polygyracea there is usually a short spermatheca and a very characteristic talon structure. Since the vast majority of the Polygyracea in the under 20 mm. size range have prominent apertural barriers, either formed at the lip edge in adults (Polygyridae) or sequentially at approximately quarter to half-whorl intervals (Corillidae), the absence of any such structures in *Craterodiscus* is another feature weighing against associating it with that superfamily.

The remaining superfamilies, the Camaenacea and Helicacea, contain a minimum of four families, the Camaenidae, Bradybaenidae, Helminthoglyptidae, and Helicidae. The last three taxa are basically Palearctic and Nearctic in distribution. They are characterized by developing various types of accessory mucous and/or dart glands on the genitalia. The Camaenidae, in the sense of Pilsbry, Thiele and Zilch, lack such accessory glands and, at most, develop a simple flagellum on the penis or epiphallus. Following Wurtz (1955), two North American taxa usually associated with the Camaenidae, the Oreohelicidae and Ammonitellidae, are considered to be distinct families, but retained within a new superfamily grouping, Camaenacea. The Camaenidae, s.s., has a disjunctive distribution. Several genera are found on the West Indian islands, while two genera, *Labyrinthus* and *Isomeria*, range from Costa Rica to Madre de Dios, Peru. In the Old World, possibly camaenid genera are known from southeastern China (*Traumatophora*, *Stegodera*, *Moellendorffia*, *Grabauia*), while definitely camaenid genera range from the Himalayan foothills of India and southern China with a few species reaching southern Japan through most of Indonesia to New Guinea, Northern Australia and the Solomon Islands. Coastal Queensland has several generic groupings that are terminal extensions of the Indonesian-Melanesian taxa, while Northern, Central and Western Australia have a major radiation of camaenid derivatives.

Unfortunately very little has been published concerning the anatomy of Indo-Australian helicoid taxa. Charles Hedley (1896, p. 224) recognized two series of genera: one (*Thersites*) with a long spermathecal duct and an epiphallic section of the male system extending above the penial retractor insertion; the other (*Xanthomelon*) with a very short spermathecal duct and the epiphallus section folded into the penis sac below the penial

retractor insertion. Wurtz (1955, p.105) has shown that in the New World camaenids there is every variation between long and short spermathecae, while the penial complex varies even more widely. The known anatomical range for the Indo-Australian camaenid taxa does not exceed that known for the New World genera. Hence the actions of Iredale (1937, 1938) in proposing the families Hadridae, Chloritidae, Papuinidae, Xanthomelontidae and Rhagadidae for Australian genera is not accepted here. All are considered to belong to the Camaenidae, *s.l.* I do not consider sufficient data available to allow subfamily recognition.

Camaenids agree with *Craterodiscus* in usually having a single mass of ovotestis tissue, frequently lacking a talon, having a closed secondary ureter, no differentiation of the mantle collar, and a pallial configuration that is consistent with being the condition from which that of *Craterodiscus* was derived. There are significant differences. All previously dissected taxa appear to have a fused sperm-oviduct and an epiphallic section differentiated from the vas deferens. Many have a flagellum on the epiphallus, although this is reduced in some taxa. Hence the separated spermiduct and oviduct, absence of an epiphallus, and no trace of any flagellar structures readily distinguish *Craterodiscus* from any dissected camaenid genera. With its long spermatheca and comparatively simple internal penial ornamentation, comparisons with the various xanthomelontid genera does not seem necessary, while the much greater size and different shape of the chloritid and hadrid stocks make conchological differences obvious. It is worth noting that the genera grouped as hadrids by Iredale average 5 - 7 whorls in adult shells, while the chloritids average $4\frac{3}{4}$ whorls and rarely reach $5\frac{1}{2}$, and the xanthomelontids are well under 5 whorls. The 6 - $6\frac{1}{2}$ whorls of *Craterodiscus* thus provide an immediate conchological separation from most genera. It should not be assumed that these whorl count differences have phyletic significance. I suspect that when enough genera have been dissected, the hadrid-xanthomelontid-chloritid groupings will be proved invalid. Most families of land snails have a rather wide range in whorl counts and these neat isolates of different whorl counts probably are artificial.

The lack of any thickening or lip reflection in *Craterodiscus* is also unusual for a camaenid and serves to differentiate it from any Australian genera. The only extralimital genus that bears close conchological resemblance is the Indian to Indonesian *Landouria*, which differs obviously in having a slightly reflected lip, many more radular teeth and a prominent epiphallus with flagellum.

Craterodiscus and *Theskelomensor* may be closely related, but until the latter has been dissected, this cannot be determined. At present, it seems best to consider *Craterodiscus* a very primitive camaenid, possibly representing character states close to the ancestral condition for the family.

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Craterodiscus

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